The Population Dynamics of the Mangrove Shrub *Aegiceras corniculatum* (Myrsinaceae): Fecundity, Dispersal, Establishment and Population Structure

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The mangrove shrub *Aegiceras corniculatum* (L.) Blanco commonly occurs in estuaries north from Merrimbula in southern NSW. Studies of the population dynamics were undertaken at Jervis Bay as part of wider baseline studies of the marine environment of the Bay. Populations in Jervis Bay flowered regularly during spring and produced viviparous fruit by the following autumn. Predispersal mortality of fruits was very high (92%), but exclusion of herbivores reduced mortality to 53%. About 360 viable propagules were produced per plant each year, representing some 32% of above-ground productivity. Once dispersed propagules can remain bouyant in seawater for up to three months, but under brackish conditions sink within a week and do not refloat. During the dispersal phase, propagules landing on intertidal sediments had a low probability of establishing because of predators and tidal disturbance. Establishment, however, appeared to be intrinsically slow because of the season in which propagules are dispersed. Shadehouse experiments also showed that propagules establish more rapidly in 10% and 50% seawater than in full seawater.

Adult populations of *Aegiceras corniculatum* were conspicuously zoned in relation to the co-occurring mangrove *Avicennia marina* (Forsk.) Vierh. The former usually occurred at the higher edge of the mangrove zone in the marine zone of the estuary, whereas populations in the riverine zone of the estuary dominated the lower edge of the mangrove zone. Establishment and recruitment appear to be episodic and highly patchy in space, although without an unambiguous measure of the age structure it is difficult to infer any population trends. Evidence from aerial photography suggests that the spatial extent of populations of *A. corniculatum* has remained static over the past 50 years, while that of *Avicennia marina* has spread. Based on broad regeneration syndromes, I predict that *Avicennia marina* would replace *Aegiceras corniculatum* under conditions of disturbance, but under long-term stable conditions the converse would apply.

Introduction

Aegiceras corniculatum (L.) Blanco, commonly referred to as the river mangrove, is a low tree or shrub that grows in the intertidal zone and has a widespread distribution throughout the shores of Australia and South-east Asia (Tomlinson, 1986). In New South Wales it is commonly found associated with, or adjacent to, *Avicennia marina* Forsk. Vierh, the grey mangrove, and it occurs in most estuaries open to the sea, northwards from its southern limit at Merrimbula (West *et al.*, 1985). The floral phenology has been described for populations in Queensland (Duke *et al.*, 1984; Hutchings and Saenger, 1987) and in NSW (Carey and Fraser, 1932; Clarke, 1994). In NSW flowering commences as early as July and is completed by December while fruits are fully developed by the following April or May (Clarke, 1994). The fruit (capsule) contains a precociously developed embryo which often ruptures the seed coat whilst still attached to the parent. Once the propagules are on

the ground the radicle penetrates the substrate and elongates and lifts the plumule. Subsequently the plumule extends through the remains of the fruit wall and the shoot emerges (Tomlinson, 1986).

Whilst there are good descriptive accounts of the floral biology of *Aegiceras* (Tomlinson, 1986), there is little information about the fecundity of plants and factors limiting fecundity. Similarly, there are many accounts of the distributions in space, especially zonations across the intertidal zone (e.g. Hutchings and Saenger, 1987; Clarke, 1993a), but studies of the population dynamics of seedlings and adults are rare (e.g. Osborne and Smith, 1990). Several studies have been undertaken to examine the growth of seedlings under glasshouse conditions, all of which show enhanced growth in dilutions of seawater (Clarke and Hannon, 1971; Ball and Farquhar, 1984).

In mangrove species with precociously developed embryos the establishment and subsequent survival of seedling populations can be studied more easily than in those plants with a post-dispersal dormant phase. In these circumstances, where there is no buried seed bank, models about establishment and recruitment to adult populations can be tested by field experiments (e.g. Smith, 1987a; Clarke and Myerscough, 1993).

The aims of this study were to: 1) determine the fecundity of *Aegiceras corniculatum*, henceforth referred to as *Aegiceras*, 2) examine factors limiting the production of viable fruits, 3) describe the dispersal properties of propagules, 4) determine what limits propagule establishment and seedling survival, 5) infer adult population dynamics from population structure and aerial photography, and 6) compare regeneration syndromes of *Aegiceras* with that of the co-occurring species *Avicennia marina*, henceforth referred to as *Avicennia*.

Methods

Fecundity

Numbers of floral buds, flowers and fruits of *Aegiceras* were followed at monthly intervals over a single reproductive season (Clarke, 1994). In total 741 buds were followed on eight trees randomly selected from widely spaced populations at Jervis Bay. The effect of predation by insects and other herbivores on the survival of fruits was assessed by bagging newly formed fruits (606) and recording the numbers of fruits that survived.

The total number of mature fruits or propagules that shrubs produced was measured by counting the number of fruits caught by litter-traps which spanned the width of individual shrubs (see Clarke, 1994). Sixteen randomly selected shrubs were sampled from widely spaced populations at Jervis Bay. Litterfall was removed from each trap at monthly intervals for three years and the numbers of intact and herbivore-damaged fruits counted.

Dispersal

The dispersal properties of the propagules were examined in buoyancy experiments that examined the effects of salinity on the buoyancy properties of propagules. Ten propagules, of the same developmental stage, from four trees were placed in treatments of full seawater, 50% and 10% seawater. The number of propagules floating or sinking was recorded at regular intervals together with the presence of the pericarp and the viability of propagules. Field observations were also made with marked propagules at two locations. At each location 20 propagules were marked with a non-toxic pen and attempts were made at weekly intervals to recover marked propagules.

Establishment and survival

Patterns of establishment of propagules and survival of seedlings were examined in two inlets at Jervis Bay. In each inlet two widely separated plots were established within

existing strands of *Aegiceras*. In each plot four 50 x 50cm cages were randomly placed and fixed so that potential predators such as fish and crabs were excluded. Thirty mature propagules of *Aegiceras* were then placed in each cage and their establishment and fates followed by 12 months. To examine the effects of predators outside the cages 30 propagules were tethered on fishing line and placed outside the cages.

A field experiment was also undertaken to examine the effect of sediment conditions on establishment. In each of two tidal inlets (Moona Moona Creek and Cararma Inlet, see Fig. 1) two plots were selected and within each area the surface sediment was either disturbed or left undisturbed. Four cages were randomly placed in each plot and five propagules of *Aegiceras* were placed in each cage.

Finally, the establishment of propagules was examined in a shadehouse experiment where thirty propagules from three locations were placed on natural sediment waterlogged with 10% seawater, 50% seawater, and 100% seawater.
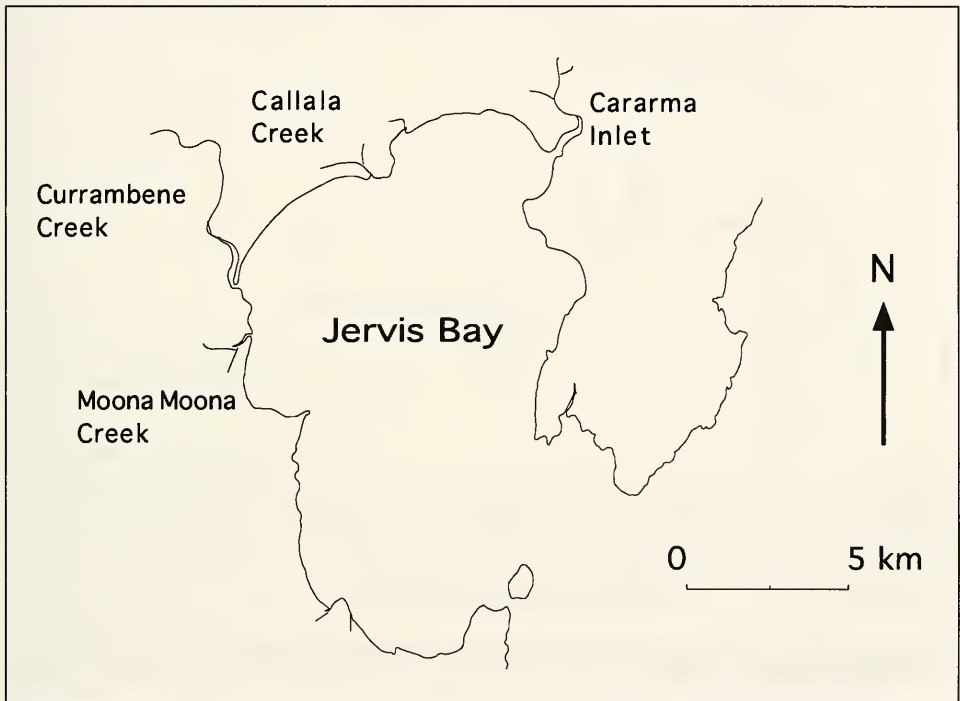

Fig. 1. Location of study sites in Jervis Bay.

Population patterns

The density and height of *Aegiceras* were measured in 22, 5 x 5m plots randomly placed within four inlets at Jervis Bay (see Clarke, 1993a). Only plants exceeding the five leaf stage were measured in this way, otherwise they were treated as seedlings and sampled differently. If seedlings were present in plots then they were subsampled with a 0.5 x 0.5m quadrat.

Where *Aegiceras* co-existed with *Avicennia* the frequency of occurrence at the waters edge or at the landward edge of mangrove stands was also recorded from 50 randomly placed transects in the upper and lower reaches of estuaries. A G-test of independence was used to test if stand locations (front or back) were independent of section in estuary (upper or lower).

<div align="center">RESULTS</div>

Fecundity

Flower buds initiate in May and the complete cycle from bud initiation to the abscission of fruits (propagules) takes about 14 months (for details see Clarke 1994). About 86% of floral buds flowered during the spring and summer months and of these about 62% formed young fruits (Fig. 2). Fruits matured over the summer months and by the time they were mature enough to produce propagules about 8% of the original flower bud population survived (Fig. 2). Bagging to exclude insects and other herbivores significantly increased survival of new fruits to 47% ($F_{1,78} = 38.6$, $P<0.001$).
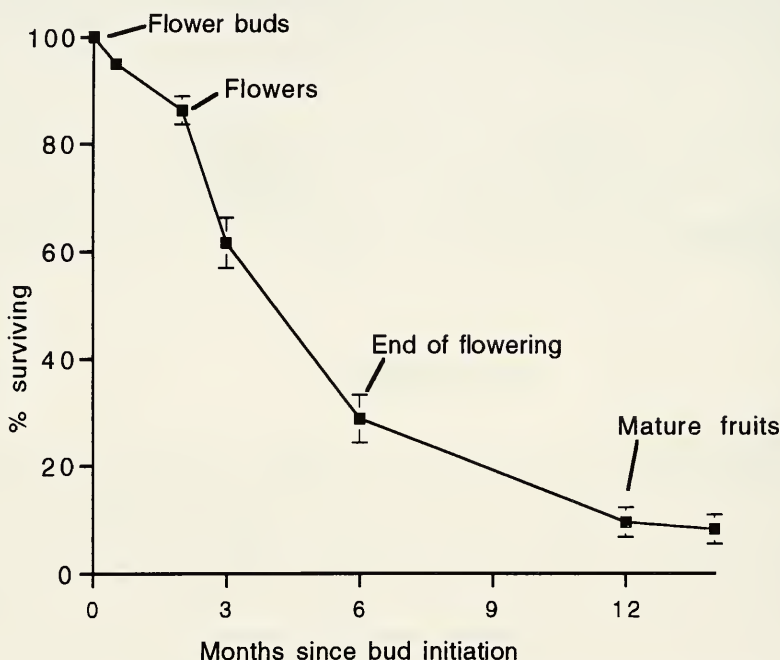

Fig. 2. Mean (s.e.) survival of *Aegiceras* flower buds, flowers, and fruits over three years and over all plants. Total number of buds followed = 740.

The total number of viable fruit and the number of mature fruits attacked by herbivores did not differ significantly year to year ($F_{2,188} = 0.98$, $P>0.4$), ($F_{2,188} = 0.58$, $P>0.5$). The mean number of viable fruits produced on an individual over three years was 356 (s.e. 44) and of these 58 showed signs of being affected by herbivores.

Dispersal

About 20% of propagules sank immediately when placed in treatments of different salinities. Of those that remained buoyant, propagules placed in 10% seawater sank sooner than those placed in 100% seawater (Fig. 3). After five days no propagules remained floating in tapwater while about half remained floating in 100% seawater (Fig. 3). Propagules placed in 100% seawater were also slower to lose their pericarps than those in 50% and in 10% tapwater. After a month all propagules had sunk and none showed any signs of decomposition. Few propagules marked and released in the field were recovered.
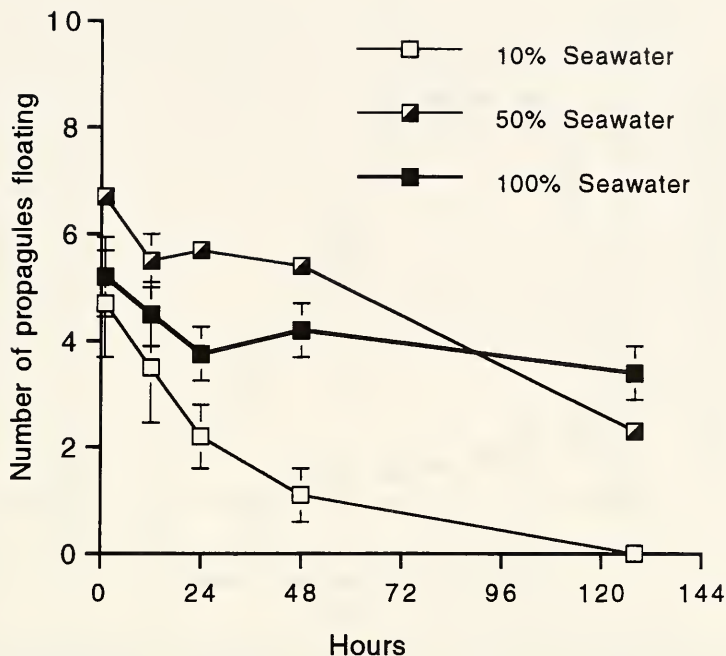
Fig. 3. Mean (s.e.) number of *Aegiceras* propagules buoyant in treatments of 10%, 50% and 100% seawater.

Establishment and survival

Less than 10% of propagules tethered in the field survived the first month and none of these managed to establish (Fig. 4). Subsequently no propagules could be found attached to their tethers. In contrast those propagules placed in cages were able to germinate (split the pericarp), and establish (Fig. 4). Overall, very few propagules actually established and produced leaves (<1%), but those that did survived for up to two years when observations ceased.

Of the 160 propagules used in the experiment to examine the effects of disturbances only five managed to establish as seedlings and all of these occurred in disturbed plots.

More seedlings established on sediments flooded with 10% and 50% seawater than with 100% seawater (Fig. 5). Propagules took up to three months to establish in all treatments but achieved their fastest establishment rates on the 10% seawater treatment (Fig. 5). In all treatments the first pair of leaves took up to six months to fully expand, thereafter when all seedlings were treated with 10% seawater for a further six months only a few seedlings developed further leaves.

Population patterns

The results from sampling adult populations have been reported elsewhere (see Clarke, 1993a). In summary, they show a highly skewed distribution with most plots containing only 1-4 plants. Adult shrubs had a remarkably normal height distribution around a mode of 60-80cm and 95% of these plants were multistemmed. Seedling densities were very high (>100m²), but were very localised as only five of the 22 plots where adults occurred also had seedlings.
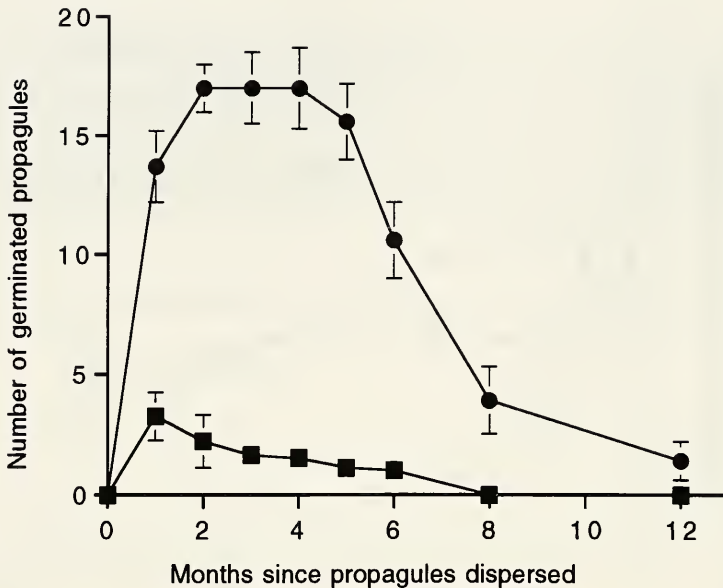
Fig. 4. Mean (s.e.) number of germinating *Aegiceras* propagules in caged ○ and uncaged □ treatments in the field. Note that no propagules established in the uncaged treatment and that a total of four propagules established in the caged treatments.

Both species of mangrove co-occurred in the 33 out of the 50 mangrove stands sampled by transects. When both species of mangrove co-occurred in stands, their position at the seaward edge of the stand or at the rear of the stand was not independent of where the stands were in the estuary ($G = 7.8$, $P > 0.01$). In other words, *Aegiceras* was more frequent at the landward edge of mixed stands in the lower estuary, whereas it was more frequent at the river edge of mixed stands in the upper estuary.

Discussion

Reproduction and fecundity

Shrubs of *Aegiceras* flower and produce fruits regularly even though the complete cycle from bud initiation to fruit abscission may overlap (Clarke, 1994). Some mortality (14%) of flower buds occurs prior to flowering and appears to result from insects burrowing into the base of the receptacle. Following a prolonged period of flowering, which possibly promotes outcrossing, many young fruits are formed. It is not known how many of these contain embryos, but bagging to exclude herbivores indicates that most contain viable fruits. The dramatic increase in survival of fruits that were bagged (47%) compared with those left unbagged (8%) indicates that herbivores have a significant effect on the fecundity of plants. This contrasts with *Avicennia* where exclusion of herbivores using bags did not increase fruit survival, although fruit set was enhanced when they were treated with insecticide (Clarke, 1992). Overall levels of fruit predation in *Aegiceras* are higher than that reported in *Avicennia* in NSW (Clarke, 1992), but are of a similar magnitude to those reported in tropical mangroves (Robertson *et al.*, 1990). Observations of fruits collected from littertraps suggest that many fruits had been attacked by larvae that enter the base of the capsule near the calyx and consume the embryo leaving only the pericarp.
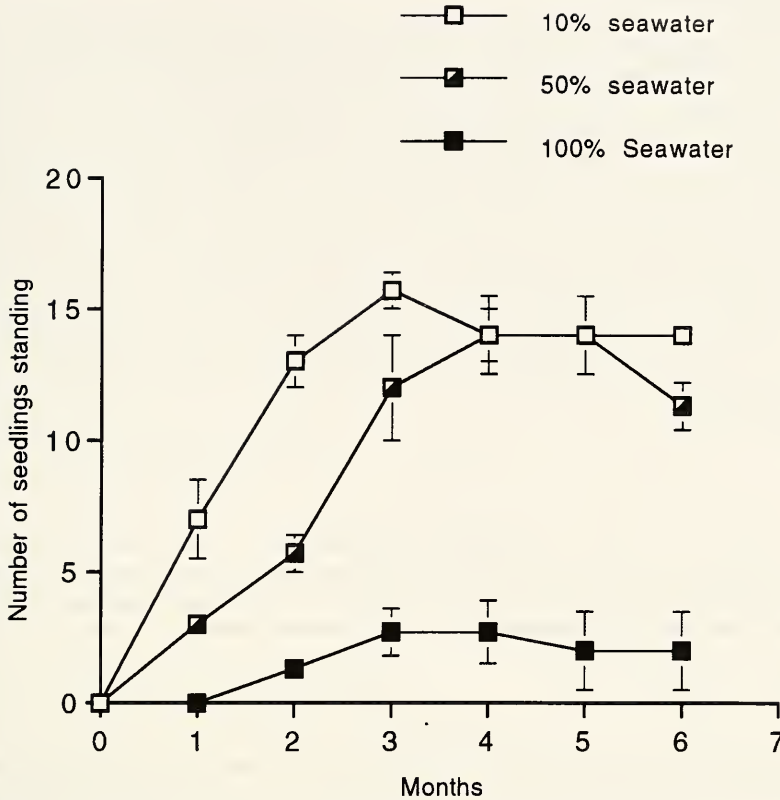
Fig. 5. Mean (s.e.) numbers of *Aegiceras* propagules establishing (standing upright) to become seedlings in shadehouse experiments over a range of salinities.

Overall, the numbers of viable propagules collected from mature shrubs of *Aegiceras* averaged c. 360 per year, thus about 4,500 flower buds per shrub are produced each year. This compares with some 61,000 flower buds and 2,000 fruits produced on a mature tree of *Avicennia* (Clarke, 1992). Nevertheless, the relative proportion of above-ground productivity devoted to reproduction in *Aegiceras* (c. 32%) is far higher than in *Avicennia* (c. 9%), which is remarkable for a perennial plant (see Harper, 1977 p. 660).

Dispersal

The dispersal phase in the life history of *Aegiceras*, like that of most mangroves, is relatively short when compared to many terrestrial shrubs because the propagules are viviparous. Factors influencing the distribution and fate of dispersed propagules include their buoyancy, period of obligate dispersal, and longevity for establishment (Rabinowitz, 1978). These factors together with abiotic (tides and currents) and biotic factors (predators and pathogens) influence not only the colonisation of new habitats but the rearrangement and replacement of populations within existing stands (Clarke, 1993b). Propagules of *Aegiceras* can remain bouyant in seawater for up to three weeks, but under brackish conditions sink within a week. This pattern is similar to that found in *Avicennia*, although propagules do not refloat under brackish conditions (Clarke and Myerscough, 1991).

Establishment and survival

Shadehouse experiments showed that the minimum time for propagule establish-ment and the transition to a seedling was at least two weeks and that propagules can take up to three months to establish, i.e. take root and lift the plumule from the ground. This establishment phase is much longer than that reported for *Avicennia*, which readily estab-lishes in the field over four weeks and up to 80% of propagules can establish when they are caged (Clarke and Myerscough, 1993). In contrast, establishment success of *Aegiceras* in the field was very low (<1%) and field observation of caged propagules suggested that propagules either failed to establish because the radicle did not develop sufficiently, or that small invertebrates consumed propagules. In the shadehouse there was a clear pref-erence for establishment of seedlings under low salinity conditions; nevertheless propag-ules took up to three months to establish and six months for the stem axis to emerge and leaves to develop. The difference between the more rapid and successful establishment of *Avicennia* and the slower establishment of *Aegiceras* possibly relates to the timing of release: the former is released during summer, whereas the latter is released during autumn in south-east Australia.

Under conditions of slow establishment, propagules of *Aegiceras* appear to be highly susceptible to herbivory as no propagules were recovered from their tethers. Similar results have been found in tropical mangrove forests in Queensland where, in the high intertidal zone, all propagules in *Aegiceras* were consumed within 14 days. However, in the low intertidal zone and in canopy gaps fewer propagules were consumed (Osborne and Smith, 1990). In the present study no such differential effects were tested, but caged and uncaged treatments were spread over a range of tidal positions, salinities, and canopy cover, and in all cases propagules appear to have been consumed.

Population patterns and processes

Adult populations of *Aegiceras* showed conspicuous patterns of distribution in rela-tion to *Avicennia* with which it commonly occurs. Populations of *Aegiceras* in the more saline parts of estuaries usually occur high on the shore, i.e. between *Avicennia* and the saltmarsh. However, those populations in the riverine parts of estuaries usually occur low on the shore, i.e. at the front of *Avicennia*. This pattern may be explained by the dispersal and establishment attributes of propagules.

Propagules of *Aegiceras* dispersed into the seawater section of an estuary remain buoyant for longer and would tend to strand at the upper tidal limits i.e. the saltmarsh. Competition from the more vigorous and larger seedlings of *Avicennia* may also displace the zone in which *Aegiceras* can exist towards the saltmarsh. In the more brackish ends of estuaries, where tidal amplitude is reduced, propagules of *Aegiceras* sink and establish faster whereas those of *Avicennia* refloat (Clarke and Myerscough, 1991) and are probably redistributed to the rear of the stand. Predators such as crabs may also influence these dis-tributional patterns, but because recruitment appears to be so episodic these models will be difficult to test in field experiments.

Rare, but dense, occurrences of seedlings of *Aegiceras* together with homogeneous adult stands suggest patchy recruitment in space and time, although the average height distribution for populations in Jervis Bay seems to indicate steady recruitment and mortal-ity, assuming height is correlated with age. Population patterns on aerial photographs support this suggestion and show that the gross distribution of adults at Jervis Bay has not changed over 50 years, while those of *Avicennia* expanded both seaward and landward. Clearly a better understanding of the age structure of adult populations and the transition rates (recruitment) between age classes is required before detailed models of population dynamics can be developed.

Finally, some general predictions can be made about how co-existing mangrove populations will interact based on regenerative attributes (*sensu* Myerscough, 1990). Both *Avicennia* and *Aegiceras* appear to reproduce regularly and at an early age relative to life-

span. Similarly, both species invest large amounts of resources into precociously devel-
oped embryos, possibly at the expense of growth and maintenance at low latitudes
(Clarke, 1994). Investment in large propagules in *Avicennia* ensures a high success rate for
establishment, whereas the propagules of *Aegiceras* are intrinsically less likely to establish,
possibly because of their smaller mass and the time of year that they are dispersed. Despite
high levels of establishment, seedlings of *Avicennia* are unlikely to recruit unless they hap-
pen upon a 'regeneration niche', i.e. an open disturbed patch (Clarke and Allaway,
1993). Seedlings of *Aegiceras*, on the other hand, do not appear to require disturbance for
recruitment as evidenced by the presence of shrubs in the understorey of *Avicennia*
stands, but are prone to extensive predation. From the limited understanding of these
population attributes I suggest that *Avicennia* would respond rapidly to disturbance and
inhibit recruitment of *Aegiceras*, as is suggested to occur in southern Queensland (Quinn
and Beumer, 1984). Under more stable conditions, especially in the upper reaches of an
estuary, populations of *Aegiceras* would establish and form dense stands in the understorey
of *Avicennia*. If stable conditions persisted then establishment and recruitment of
Avicennia seedlings would be inhibited and eventually the stands would be dominated by
Aegiceras until the next disturbance.

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